POLYXYLIC STEM OF CYCAS MEDIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 252

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(WITH ELEVEN FIGURES)

The question which lends particular interest to the polyxylic situation in 4 of the cycad genera (*Cycas*, *Macrozamia*, *Encephalartos*, and *Bowenia*) is whether or not the separate, concentric. vascular cylinders all originate with the differentiation of procambium strands in the plerome cylinder, and whether or not true protoxylem and protophloem are formed in every or in any instance. If protoxylem and protophloem are formed, are they or are they not orthodox in their detailed structures, and what is their condition in the older parts of the stem?

It is the purpose of this investigation to discover the exact origin and behavior of the different cambiums which develop the separate vascular cylinders, and to formulate some definite conclusions regarding the vascular elements which will leave the matter of this unusual method of secondary growth more clearly understood.

Historical

Although research among the cycads has been comparatively limited by lack of suitable material for study, several accounts have been published which deal more or less directly with the present problem. During an investigation of *Cycas siamensis* in 1885, Constantin and Morot[1] concluded that the cambium of each supernumerary zone, laid down outside the first or normal cylinder, originated in the pericycle of the cylinder next inside.

In 1896 Wordsell[2] published an account of the polyxylic stem of *Macrozamia*. In this particular genus he found the corti-

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[1] Constantin, J., and Morot, L., Sur l'origine des faisceaux libéro-ligneux supernuméraires dans la tige des Cycadées. Bull. Soc. Bot. France **32**:173. 1885.

[2] Wordsell, W. C., Anatomy of stem of *Macrozamia* compared with that of other genera of Cycadeae. Ann. Botany **10**:601–620. 1896.

cal cylinders diminishing in the thickness of their wood and phloem as they neared the tip of the stem, until finally they disappeared entirely, the outermost disappearing first and the innermost last. Protoxylem, at least of the spiral kind, he found to be entirely obliterated in the normal cylinder, although it seems to have been of frequent occurrence in the leaf traces, where the crushing pressure of thickening cells was less effective. He mentions no protoxylem in connection with the supernumerary cylinders, either as to its presence or absence, nor in connection with leaf traces coming from these cylinders.

Scott's[3] work in 1897 led him to the conclusion that the polyxylic habit was a derivation from the habit of ancient stems among the Cycadofilicales which developed layers of concentric bundles, for example, *Medullosa*.

Wordsell[4] again in 1900 published an account of the seedling stem structure in *Bowenia*. There he found beginnings of a supernumerary vascular cylinder outside the normal one. Hints of concentric bundles, which he found in *Bowenia* and earlier in *Macrozamia*, led him to agree with Scott in the idea of the phylogenetic origin of supernumerary cylinders.

Coulter and Chamberlain[5] published in 1910 a summary of previous investigation pertaining to the vascular anatomy of cycad stems, and in addition gave a short description of the gross topography of the polyxylic habit.

Jeffrey's[6] work, published in 1917, is the most recent account of this cycad peculiarity. To him also it is apparent that supernumerary cylinders arise in the pericycle. He objects, however, to Scott's conclusions in regard to the phylogenetic origin of these vascular cylinders; he believes rather that they are a result of an ancient climbing habit of the stem. Such situations, he says, are frequent in numerous climbing stems of the present time, stems of both gymnosperms and dicotyledonous angiosperms.

[3] Scott, D. H., The anatomical characters presented by the peduncles of Cycadaceae. Ann. Botany **11**:399–419. 1897.

[4] Wordsell, W. C., The anatomical structure of *Bowenia spectabilis*. Ann. Botany **14**:159–160. 1900.

[5] Coulter, J. M., and Chamberlain, C. J., Morphology of gymnosperms. 1910.

[6] Jeffrey, E. C., The anatomy of woody plants. 1917.

The foregoing brief account of previous research, touching upon the problem at hand, gives a foundation upon which to work and from which to develop further lines of investigation.

Material and methods

Material used in the study of the problem was collected by Dr. CHAMBERLAIN near Rockhampton in Queensland, Australia. I take this occasion to express my appreciation of his generosity in giving up material from his own private collection for my study, and of his helpful suggestions during the investigation. The plant collected by CHAMBERLAIN was about 3 m. in height, as it occurred in nature, and bore at its tip a cluster of megasporophylls surrounded by a crown of foliage leaves. Two pieces were taken from the stem, one at the apex and one near the base. The former piece was the entire tip, including the upper 6 or 8 inches of the axis, together with foliage leaves and megasporophylls; the latter piece was a cross-section of the stem at a height of less than a foot above the soil, and was cut with a thickness of about 3 inches. Both pieces were put into formalin, where they have remained since the time of their collection in November 1911.

Pieces of the stem were thoroughly washed in water and then allowed to stand in 50 per cent hydrofluoric acid for a period of 4 weeks. Following this treatment, methods were employed which were based upon the fundamentals of technic as published by CHAMBERLAIN[7] in 1916. Such variations in these principles as were used grew out of the kindly suggestions of Miss LANGDON of this laboratory. To her my thanks are given for her valued assistance.

Investigation

GROSS TOPOGRAPHY

As would be expected, the pith of this specimen is relatively large. Its diameter at the stem base measures 5.3 cm., whereas the diameter of the entire stem at the base is only 20 cm. At the tip, where the gross diameter is 17.8 cm., the pith has a diam-

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[7] CHAMBERLAIN, C. J., Methods of plant histology. 1916.

eter of 5.8 cm. There is practically no tapering to the columnar trunk excepting at the very apex, while the pith actually increases in diameter as it nears the apex, until it finally merges into the plerome cylinder (fig. 1).

At the base of the stem there are 3 separate and distinct vascular cylinders, the normal one nearest the pith and the 2 cortical ones developed concentrically about the normal. In previous accounts the first cortical cylinder has been reported to have a development of xylem and phloem equal to that of the normal cylinder, while the second and succeeding cortical cylinders diminish successively in that development toward the periphery of the stem. I find in this stem, however, that, near the base, the first cortical cylinder has a greater radial extent of xylem and phloem than has the normal one, while the second is about the equal of the normal, thus beginning the successive decrease of xylem and phloem development which would likely be continued further if other vascular cylinders were present (fig. 2). In each cylinder the xylem elements are of greater radial extent than phloem elements, the former occupying approximately three-fifths of the radial extent of the entire cylinder.

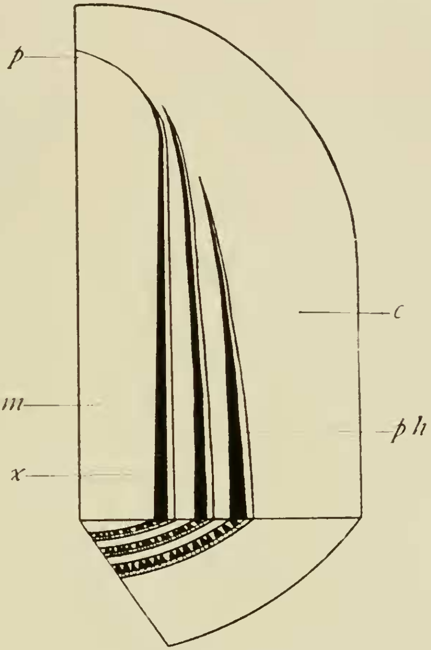

FIG. 1.—*Cycas media:* showing radial and transverse aspects of polyxylic stem near tip; *m*, pith; *p*, plerome; *x*, xylem; *ph*, phloem; *c*, cortex.

At the stem apex only 2 vascular cylinders are evident (fig. 3). Here the normal cylinder is seen to have xylem and phloem of slightly less radial extent than it has near the stem base, while the first cortical cylinder has decreased so much in its dimensions that it is barely visible to the unaided eye. Furthermore, the latter occurs, not as a continuous cylinder, but rather as a cortical layer of separate, broad, and short bundles which are distinctly collateral. The outermost cortical cylinder entirely disappeared before reaching the height at which the section was taken. This quite agrees with WORDSELL'S (*loc. cit.*) account of a situation exactly similar in *Macrozamia*. Fig. 1 represents the polyxylic structure diagrammatically, as it might be seen in radial section in the apical region of the stem. Differentiation which results in cortical cambium begins farther from the stem apex in each succeeding cylinder, being farthest in the outermost cylinder.

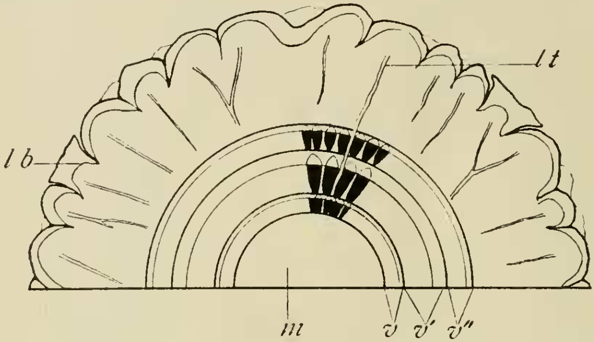

FIG. 2.—*Cycas media:* showing gross topography of transverse section of stem near base; *v*, *v′*, *v″*, 3 distinct vascular cylinders; *m*, pith; *lt*, leaf traces; *lb*, leaf bases.

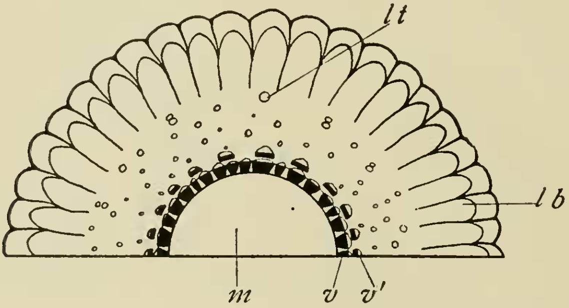

FIG. 3.— *Cycas media:* showing gross topography of transverse section of stem near tip; *v*, *v′*, 2 vascular cylinders; *m*, pith; *lt*, leaf traces; *lb*, leaf bases.

The cortex, true to cycadean character, is relatively large, as well as the pith. At the stem base the cortex measures 2.9 cm. between the outermost cortical cylinder and the leaf base, and at the tip 2 cm. A great many leaf traces traverse the cortex. At the base of the stem these traces are seen in longitudinal section (fig. 2), excepting at those places where they are just leaving the vascular cylinder. At the tip, however, leaf traces are invariably seen in transverse section (fig. 3), and they are characteristically double where they are about to enter a leaf base. Traces may leave any or all of the vascular cylinders, those from the inner ones passing to the cortex through the medullary rays of one or more outer cylinders.

DETAILED STRUCTURE

Normal cylinder.—Vascular bundles of the normal cylinder are long and narrow in transverse section (fig. 4), rarely becoming more than 3 or 4 cells in tangential thickness. Bundles taper to a rather sharp point toward the pith, and there is located the definite endarch protoxylem. Wordsell had difficulty in locating protoxylem in the stem of *Macrozamia* which he studied, for it had been obliterated by the crushing caused by thickening wood cells. In the specimen which I studied the protoxylem is still intact in the majority of cases, and is easily distinguished (fig. 4). Fig. 5 represents protoxylem of the normal cylinder, enlarged enough to show its detailed character. The cell walls are less thickened than those of the primary xylem above, and there are certainly no pits present, as there would be if the xylem were of secondary origin. In this particular instance pits are absent from the primary xylem also. This is an unusual condition, since, as in fig. 6, primary xylem of the normal cylinder is practically always scalariform. Fig. 6 shows the radial aspect of the normal cylinder in its centripetal region. Here protoxylem elements are unquestionably spiral in character, while the succeeding primary xylem is scalariform. It should be said here that spiral tracheids are of comparatively rare occurrence even in the normal cylinder; at least they are rare in stretches large enough to be correctly interpreted. The usual form of protoxylem is scalariform rather than spiral. Since neither transverse nor radial preparations show crushed masses of cellular material at the centripetal ends of bundles, there can be no doubt that the xylem elements which can be seen to terminate the bundles are truly protoxylem, whether they are spiral or scalariform.[8]

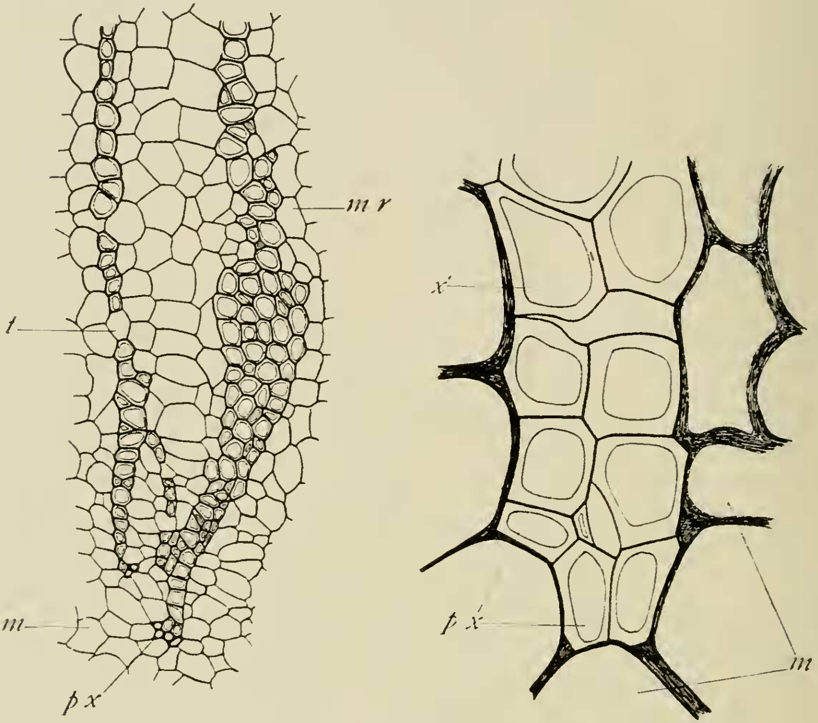

FIG. 4 FIG. 5

FIGS. 4, 5.—*Cycas media:* fig. 4, transverse section of stem, showing only centripetal end of bundle of innermost cylinder; *m*, pith; *mr*, pith ray; *px*, distinct protoxylem; *t*, unthickened xylem elements; ×400; fig. 5, transverse section of stem, showing centripetal end of bundle of innermost cylinder highly magnified; *m*, pith; *px*, protoxylem; *x′*, primary xylem; pits apparent in none of these cells; ×850.

As in WORDSELL'S account, spiral tracheids here can be followed more easily in leaf traces off the normal cylinder than they can in the cylinder itself. The reason for this is not that these elements have been destroyed in the cylinder proper, but that

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[8] CHAMBERLAIN, C. J., The adult cycad trunk. BOT. GAZ. **52**:97. 1911.

they meander back and forth tangentially, so that only short patches can be caught here and there in a single radial section. The meandering habit is not so pronounced in the traces, and consequently longer stretches of primitive xylem elements can be seen and identified as such.

Secondary xylem of the normal cylinder is composed of tracheids which are characteristically pitted, the pits being confined largely to the radial walls, as described by both Chamberlain and Jeffrey.

The phloem situation of the normal cylinder adds emphasis to the fact of the latter's procambium origin, for protophloem is as distinct here as it is in any of the typical monoxylic cycad stems. Fig. 7 illustrates the upper phloem region of this cylinder, showing the crushed cellular substance which once was organized protophloem. This dark crushed mass has the appearance of a thick irregular ring in transverse section, entirely surrounding the normal cylinder and immediately inside the centripetal limits of the first cortical cylinder (fig. 8). The ring of course is interrupted here and there by medullary rays, but in many cases it extends unbroken across them, being squeezed in between the cells of the pith or cortical medulla. From this protophloem center primary and secondary phloem extend, fanlike, outward and downward in typical fashion. The rather startling character of the secondary phloem is its large number of suberized bast fibers compared to the number of sieve tubes. The former far

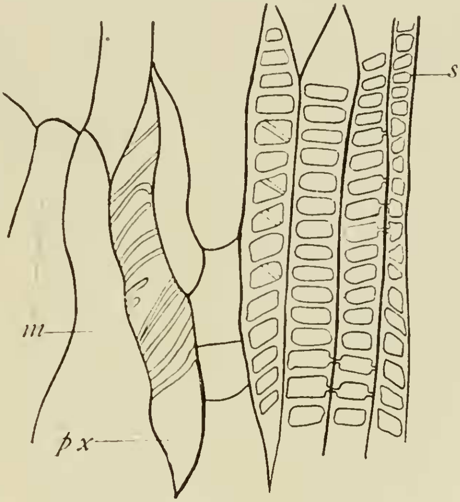

Fig. 6.—*Cycas media:* radial section of stem, showing centripetal end of bundle of innermost cylinder; *m*, pith; *px*, protoxylem distinctly spiral; *s*, scalariform tracheids of primary xylem, left one also having spiral thickenings; ×400.

outnumber the latter, which occur here and there in short tangential rows between the bast.

First cortical cylinder.—The most intensive study of the cortical cylinder was made from preparations of the innermost one near the apex of the stem (fig. 3). Here details could be observed where the cylinder was in an early stage of development, and where its character could best be determined.

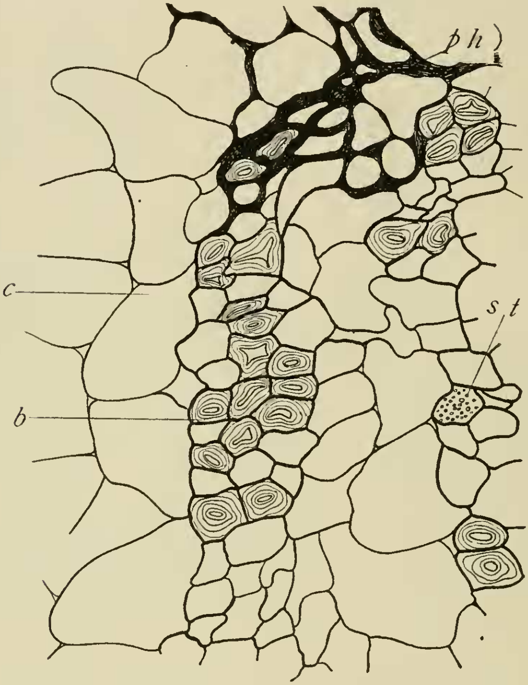

Fig. 7.—*Cycas media*: transverse section of stem, showing region of protophloem of innermost cylinder; *ph*, protophloem; *b*, suberized bast fibers of secondary phloem; *st*, sieve tube; *c*, cells of cortex; ×235.

Fig. 8 shows a transverse section of the entire cylinder, together with regions bordering it on both inner and outer boundaries. Apparently no protoxylem is present in these bundles. Cells at the centripetal limit of a bundle are not different from those nearer the cambium; there is little or no difference in size, shape, and thickness, in alignment, or in the character of cell walls. Fig. 9 shows characteristics of the xylem in that region of the cylinder where protoxylem would be expected if there were any. All cells are uniformly thickened and, without exception, equipped with bordered pits, which is always a mark of secondary origin. In fig. 10 the same region is seen in radial section. Here the xylem element nearest the stem center, and even bordering on protophloem of the normal cylinder, is pitted. This one drawing illustrates tracheids of the first cortical cylinder which are as nearly scalariform as could be found; they are as rare as spiral tracheids are in the normal cylinder. By far the greater number of xylem elements in this centripetal region of the cylinder are pitted in exactly the same fashion as ordinary secondary tracheids of the normal cylinder, and they must in turn be considered as of secondary origin.

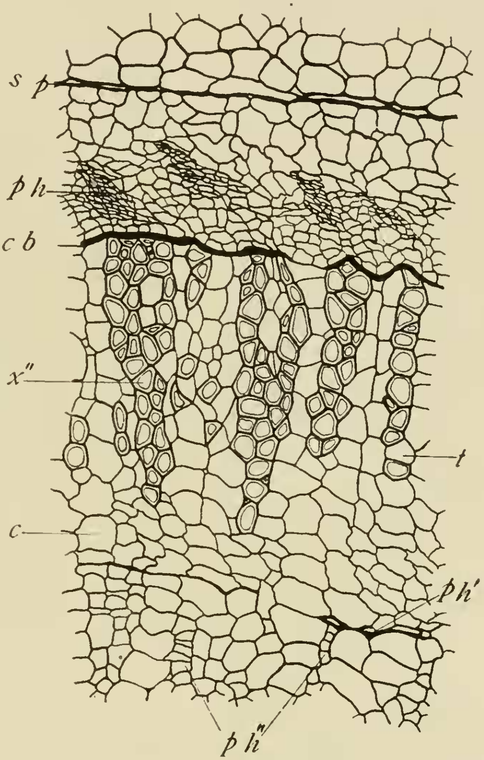

Fig. 8.—*Cycas media:* transverse section of stem, showing entire second cylinder as it appears near tip of stem; *ph'*, protophloem of first cylinder crushed; *ph''*, secondary phloem of first cylinder; *c*, cortical cells; *x''*, secondary xylem of second cylinder; *t*, unthickened xylem cells; *cb*, cambium; *ph*, secondary phloem of second cylinder; *sp*, split in cortex caused by expansion lower down of third cylinder; ×85.

In fig. 8 it will be seen that the region between the normal cylinder and the first cortical one is composed of purely cortical cells. Also the region between the first cortical cylinder and the split in the cortex, which marks the place where the second cortical cylinder will appear, is purely cortical. No differentiation is evident between stelar pericycle and cortex; there is even no endodermis, and therefore there is no ground here for believing that the supernumerary cylinders originate in the pericycle. In view of Sister Helen Angela's[9] work with *Ceratozamia*, in which she found unquestionable cambiums at any place in the cortex from the stele to the periphery, it would be possible for the supernumerary cylinders of *Cycas* to originate in the cortex. In view of the evidence of fig. 8 it would also seem probable that the cylinders are truly cortical and not stelar.

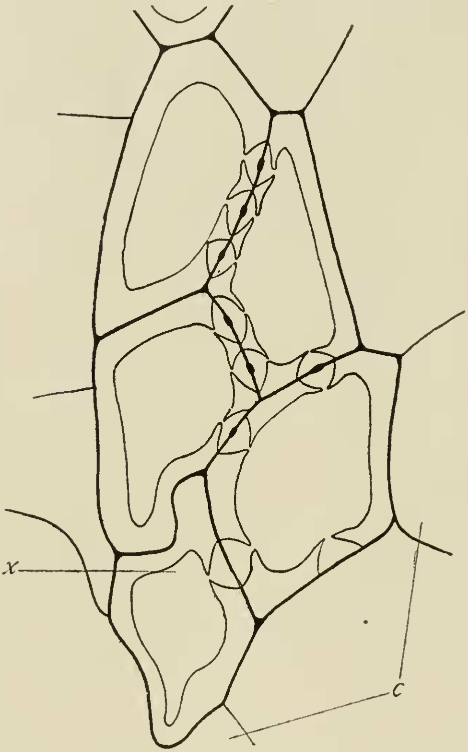

Fig. 9.—*Cycas media:* transverse section of stem, showing centripetal end of second cylinder; *c*, cortical cells; *x*, distinctly pitted xylem cells at tip of bundle; ×850.

There is no evidence of protophloem in connection with the cortical cylinder. A transverse section (fig. 11), which is thoroughly representative of the state of affairs, shows that practically all cells of the phloem are suberized bast fibers. This, together with the very apparent alignment of the fibers, is convincing proof that no protophloem is present.

Sections of the first cortical cylinder near the stem base reveal conditions almost identical with those of the normal cylinder, excepting that in the former both protoxylem and protophloem

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[9] Dorety, Helen A., The extrafascicular cambium of *Ceratozamia*. Bot. Gaz. 47:150–152. *pl. 7.* 1909.

are absent. Bundles of the former resemble those of the latter in shape, the secondary alignment of the former being disturbed by unequal growth and pressure, and bundles of both are of about equal size, those of the cortical cylinder being a little longer radially. Both cylinders give off leaf traces which differ in respect to the presence or absence of protoxylem and protophloem.

OTHER CORTICAL CYLINDERS.—There is little reason for believing that the second and succeeding cortical cylinders would have a mode of origin and development different from that of the first; consequently but little time was devoted to the study of the second cortical cylinder. Preparations from the stem base only were examined, and, as was expected, these showed conditions in the mature part of the stem identical with those of the first cortical cylinder in the same region. Further discussion, therefore, would be but a repetition of what has been recorded thus far.

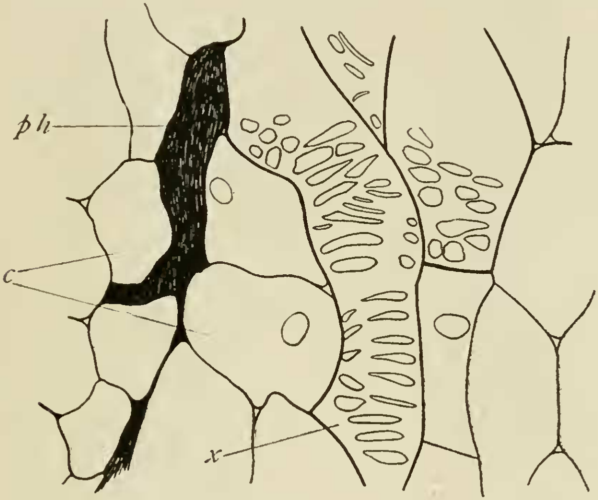

FIG. 10.—*Cycas media:* radial section of stem, showing centripetal end of second cylinder; *c*, cortical cells; *ph*, crushed protophloem of first cylinder; *x*, innermost xylem elements of cylinder, showing distinct pits, some having fused; ×400.

In concluding the matter of cortical cylinders it may be well to mention the relationship of their number to the age of the plant. Certainly they do not occupy the position of growth rings, nor are they laid down at regular intervals of time. The plant which was studied was more than a century old and yet had but 3 vascular cylinders. Doubtless the cortical cylinders are related to certain activities of the plant alternating with long periods of rest which may vary greatly in point of duration.

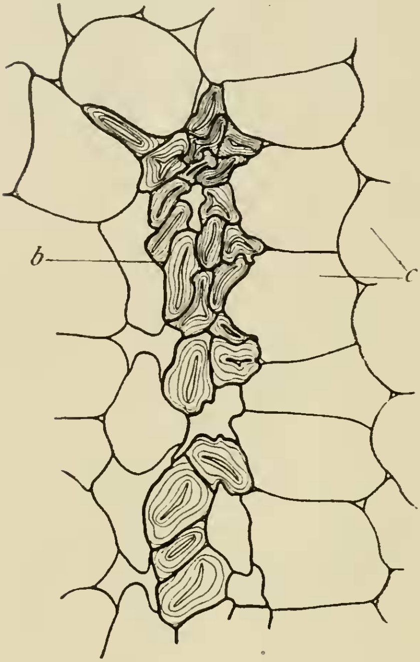

FIG. 11.—*Cycas media:* transverse section of stem, showing tip of phloem belonging to second cylinder; *c*, cortical cells; *b*, suberized bast fibers; ×235.

Summary and conclusions

1. The paper deals with the adult stem of *Cycas media*, particular attention being paid to the xylem and phloem details of the normal and first cortical cylinders.

2. Not all the vascular cylinders are of equal longitudinal extent. Only the normal one begins its differentiation as high up as the meristem, the others beginning their differentiation successively lower, and each one in the cortex outside the next inner cylinder. The normal cylinder, therefore, is the only one which would be expected to originate with a procambium, and the only one which could develop protoxylem and protophloem.

3. Following up these expectations, both protoxylem and protophloem were found to have been developed during the early activities of the normal cylinder. Protoxylem elements are usually scalariform, although hints of spiral tracheids are more or less frequent. Primary xylem is scalariform and secondary xylem is characteristically pitted.

4. Neither protoxylem nor protophloem was found in the first cortical cylinder. Practically all of the xylem elements are pitted, but scalariform tracheids are occasional.

5. The secondary phloem of both cylinders is characterized by the great number of suberized bast fibers compared to the number of sieve tubes.

6. All cortical cylinders are similar in respect to their origin and development and are probably related in their appearance to the alternating periods of rest and activity of the plant.

7. Unfortunately material was unavailable which would have shown the beginning of differentiation of a cortical cambium. Such a piece taken from the stem apex would have been far enough up to destroy material needed for further research.

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